# THE PHENOGAMOUS PARASITES

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THE object of this essay is to describe in a popular manner the chief characteristics of the known kinds or groups of phenogamous parasites, to show their relation to one another and to normal phenogams, and to discuss their structure and habits with reference to the probable manner of their origination. In order to make a popular statement of the characteristics of each group of these abnormal plants and to discuss them clearly it is first necessary to summarize briefly the elemental structure and physiological characteristics of the normal phenogams. I have chosen to do this in verbal terms a part of which are somewhat unusual, but which are believed to be specially appropriate to discussions of this kind.

The elemental parts of a normal phenogamous plant are root, stem and leaves, the beginning of the differentiation of which structures is distinguishable even in the embryo; and to these are added, at the maturity of the plant, flowers and fruit. Every normal phenogam also consists of two incremental parts, an up-growing and a down-growing part, respectively, the latter entering the soil to form the roots. The normal phenogamous plant performs all its physiological functions within, and for, itself and lives independently of all other plants except in the matter of competition with them for the benefits of soil, moisture and sunlight, but the parasites escape the performance of those functions so far as nutrition is concerned. The normal plants derive the materials for their subsistence and growth from inorganic sources and elaborate them within their own tissues for their own use, producing thereby their new organic substance, but the parasites rob other plants of that substance in its elab-

orated condition. The supply of inorganic material is obtained by normal plants partly in a soluble and partly in a gaseous condition, the former being contained in the food-sap which the roots derive from the soil, and the latter in the atmosphere which surrounds the plant. The function of the root requires a constant accession of moisture, and that function is vital with relation to the other functions of the plant presently to be referred to. The action of sunlight is indispensable in the condensation and elaboration of those inorganic materials into new organic substance. An essential step in that elaboration of new material is the production of chlorophyl, which takes place partly in the bark of the growing branches, but mainly in the parenchyma of the leaves. Fully developed green leaves are therefore among the chief organs of normal phenogams, and their absence from the greater part of phenogamous parasites is due to the inability of those plants to produce chlorophyl. It is for these reasons that chlorophyl is so frequently mentioned in the following paragraphs.

The reproduction of normal phenogams is by two methods, namely, parturital [1] and blastemal.[2] These methods have such relevancy to the subject in hand that it will be frequently necessary to refer to them. The first is the conjugative method and provides for the hereditary transmission of specific and other systematic characters, the geographical distribution of species and the multiplication of individual plants. It is periodically cyclic, the maturation of the seed ending one cycle and the germination of its embryo beginning another. The second is the autogenous method and pertains to the growth and preservation of the individual plant. Its operation is physically continuous during the whole life of the plant, and every bud of the plant is connected with all the other buds by living somatic cells. The horticultural processes of budding and grafting consist of transferring blastemal

[1] Parturio, to bring forth young.

[2] Βλαστος, a bud. These terms are regarded as preferable to "sexual," "asexual," "vegetative," etc., which are often used by writers.

reproduction from one plant to another. They are closely simulated by some parasites in their manner of attachment to the host, but there are radical differences between parasitic attachment and horticultural grafting.

The two incremental divisions of every normal phenogam consists of an epitropic, and an apotropic[3] portion, respectively, separated by the tropaxis. The epitropic portion, beginning with the radicle at germination, enters the ground, divides into roots and rootlets, and establishes the plant in position. This is primary epitropism. The apotropic portion at the same time extends upward, forming the stem and finally the branches, leaves and fruit. This is primary apotropism. The tropaxis is a theoretical disc at, or a transverse section of, the base of the stem from which growth proceeds in opposite directions. Its functional existence as a dividing plane is real and constant during the life of the plant, but it is structurally not clearly definable. That is, no material change of plant-texture occurs at the place where the upward and downward growth diverge, and no obstruction to the flow of food-sap from one to the other portion exists there. Suckers, stolons, sprouts, etc., sometimes spring from roots, root-stalks or tubers, and become new plants. This is secondary apotropism. Roots or rootlets often spring from the stem or branches. This is secondary epitropism. A new or secondary tropaxis is formed in every case of secondary apotropism at the place where the upward growth begins and new roots turn down into the soil.[4]

Such are the leading structural characteristics of normal phenogamous plants, which constitute the mass of

[3] For a full explanation of these and some of the following terms see my article in *Science*, N. S., vol. XII, pp. 143–146.

[4] The terms "hypocotyl" and "epicotyl," meaning below the cotyledons and above the cotyledons, respectively, often have been used by authors to designate the apotropic and epitropic portions, respectively, of the germinating embryo. Those terms are inappropriate for such use because the place of attachment of the cotyledons rarely, and only accidentally, coincides with the place where upward and downward growth diverge, and the two places are often far apart. A case in which they are far apart is illustrated by the plantlet of Convolvulus as shown by Fig. 6, on page 28.

the green vegetation of the earth. Abnormal phenogams constitute only a very small proportion of the great mass of vegetation, and yet the aggregate number and variety of their forms is really very great. Three general kinds of abnormal phenogams are recognized, namely, parasites, saprophytes and symbionts. They have certain characteristics in common and often are visually similar, but they differ materially from one another in the manner of procuring their subsistence, and the habit of each of them in that respect may be either partial or complete. That is, a phenogam may be partially parasitic, saprophytic, or symbiotic, and partially normal; or parasitism may be associated in one and the same plant with saprophytism. While my chief object is to discuss the parasites, it will aid in defining their characteristics to present a brief statement of those of the two other kinds of abnormal phenogams.

Saprophytes derive their subsistence from dead organic matter in the soil which has not reached the stage of full decomposition. That matter yields a soluble portion to the food-sap which the plant obtains by its roots in the usual manner and, after some reelaboration, that portion is applied by the plant as new organic substance in the building of its tissues. Saprophytes, like vultures, hyenas and epicures, take their food in a partially decomposed condition and thrive upon it. Doubtless many plants that are properly regarded as normal are really in part saprophytic when their roots have access to organic manures, but only completely saprophytic phenogams are here referred to. It is claimed by some investigators that completely saprophytic phenogams sometimes produce chlorophyl and develop green leaves, but those here discussed produce no chlorophyl, develop no functional leaves, and are therefore not green in color. Their reproduction, both parturital and blastemal, is normal and they grow from their roots in the soil like normal plants, with none of which are their vital relations antagonistic. Completely saprophytic phenogams, which only are now particularly referred to, are comparatively rare, especially in ordi-

nary soils. They are mostly confined to swampy and other moist soils that contain much decomposing vegetable matter, and to shady positions. It may be suggested that the abundance of disintegrating organic material contained in the soil in which these completely saprophytic plants grow furnishes so large a supply of material which is still useful for assimilation in the production of new organic substance that the entire leaf-function, including the production of chlorophyl, is suspended as being superfluous, and that this habit has become permanent and hereditary.

Completely symbiotic phenogams live in enforced vital union with a fungus which adheres to and covers its roots, and through which it derives all its soil-subsistence. The roots being entirely enveloped, their normal function is destroyed and the fungus also assumes the office of purveyor of nutriment. As do other fungi, it obtains that food-material from decomposing organic matter in the soil and transfers a portion of it to its consort through their surfaces of contact. Although that food-material, when obtained by the fungus, is partially decomposed, and is received at second hand by the captive phenogam, the latter thrives upon it, and, its above-ground portion being free, the functions of vegetative growth and reproduction are normally performed. Its leaves, however, are abortive or functionless and never green in color, for completely symbiotic phenogams do not, and do not need to, produce chlorophyl. Their failure to do so is doubtless a direct result of the condition which is imposed upon its roots by its fungus consort. The vital relations of these strangely modified phenogams with other plants are normal, but their condition with relation to the fungus is apparently that of pitiable captivity. The usurpative control of their nutrition by the fungus suggests that these phenogams did not originate as symbionts by a predilective departure from a self-supporting condition. Partial symbiosis of fungi with phenogams is not uncommon and is understood to be, at least in many cases, mutually beneficial, but it has only incidental relevancy in

this connection. One can hardly doubt that the complete symbiotic condition of those plants has been imposed by the aggressive increase of the fungus from its original condition of partial symbiosis, but the phenogam so fully acquiesces in it that the deficiencies of structure and function which its imposed condition entails have become harmonious with that condition and hereditary. Even the embryo, at least in the case of Monotropa, or Indian pipe, and probably also in that of Sarcodes, or the snow plant of California, has lost its differentiation into cotyledons and plumule. This is a significant coincidence with a similar condition which prevails in the embryo of many parasites, as will be shown in following paragraphs.

Examples of complete symbiosis are few among phenogams, the most common case being that of Monotropa. All the older botanists believed, and some of them so stated in their text-books, that the species of that genus are parasitic upon the roots of woody plants. Later authors often have stated that Monotropa is saprophytic, but still later investigators have demonstrated that the plants of this genus are completely symbiotic. It will be a disappointment to the older plant-lovers not to find their familiar acquaintance, the Indian pipe, discussed among the parasites on the following pages, but the facts which have been stated require its omission there.

Whatever view one may take concerning the two kinds of abnormal phenogams that are briefly defined in the preceding paragraphs, he instinctively regards the parasites as a criminal class in the great community of honest plants. Their methods of parasitism are so varied, and each method is prosecuted with such vigor and constancy, that it is necessary to review them with reference to those habits rather than to similarities and differences of systematic structure. They all are at least acquisitive in their relations with other plants, and some of them are vigorously aggressive and raptorial. They all derive new organic substance from other plants, always from living ones, and apply it directly in the building of their own tissues. Some of them are annual, and some

perennial. Some are herbaceous, and some woody. Some of them attack only the epitropic, and some only the apotropic, portion of their host. Some are only partially parasitic, obtaining only a part of their subsistence in that manner, but a large number are completely parasitic, and thus obtain their entire support from other plants. The former obtain a part of their subsistence from the soil as normal plants obtain all of theirs. They also develop leaves and produce chlorophyl, but the complete parasites, with exceptions to be mentioned, develop no functional leaves and produce no chlorophyl, for completely parasitic plants do not need to produce it. New organic substance, elaborated as already has been mentioned, is of course necessary to the existence of the normal plants which produce it. It is no less necessary to the existence of the parasites, but they, not being able, or not predisposed, to produce it for themselves, obtain it by robbery from other plants. All of them are so depraved that they acquire special hereditary habits of rapine, modify their structure, and even develop special organs with which to accomplish their thefts. The deficiencies and modifications of structure are correlated with the respective kinds of parasitism, and they are invariable and heritable. Even the embryo of some of them is structureless, not being differentiated into cotyledons, radicle and plumule. Indeed, some of the most vigorous of the parasites originate from embryos that apparently represent only a moiety of the normal phenogamic embryo.

The leaves of normal phenogams are properly regarded as the chief organs concerned in the production of chlorophyl, but if my assumption is correct that the agency of a structural root is a precedent necessity in normal cases of such production, the functional leaflessness of a parasitic phenogam is a direct consequence of its rootlessness. That is, because a rootless phenogam can produce no sufficient quantity of chlorophyl, and because it procures its new organic substance by theft, it has no use for leaves. Therefore, those leaves which it morphologically inherits remain undeveloped or functionless. This is the

condition of complete parasitic phenogams, but those which are only partially normal supplement their honest gains by theft. They are all robbers, and obtain new organic substances from their hosts by methods which resemble grafting, budding and leeching, respectively. In the first two cases mentioned the embryo of the parasite is thrust into the living tissue of the host from which the resulting parasitic plant draws its nourishment, much as do the bud and scion in cases of budding and grafting. In the other case special organs, namely, haustoria, are developed as instruments of robbery. These organs serve to draw new organic substance in liquid form from normal plants, and they are as indispensable to the parasite which possesses them as are roots to normal plants. They are produced as small outgrowths from different parts of different parasitic species, sometimes upon the roots and sometimes upon the stem and branches. They are of wart-like, discoid, globular, or more or less irregular form, and are sometimes single and symmetrical, but oftener in groups or clusters and shapeless masses. When single they are sometimes sessile and sometimes terminal on slender pedicels. They attach themselves by their free surface to the host, and so burrow into its subcortical and subcortical tissues that the growing cells of both plants are intimately commingled. Acting like suckers, they withdraw in liquid form the new organic substance which the host had prepared for its own use, much as a leech extracts blood from its victim. The haustoria of parasites are comparable with roots of normal plants because, like roots, they are the instruments by means of which the plants obtain necessary supplies, but true haustoria are not roots nor morphological representatives of them.

The foregoing remarks apply mainly to the general characteristics of the parasites as compared with saprophytes, symbionts and normal plants. The special characteristics of the parasites are grouped and briefly summarized in the following synopsis. In remarks which follow each synoptical statement some of the more con-

spicuous of those extraordinary habits which members of the various groups possess and which have become constant and hereditary will be shown. Many of those habits are of wonderful character, and one almost feels that he is dealing with sentient beings of great cunning and lawlessness rather than with vegetal forms.

The phenogamous parasites are so aberrant as regards both their structural and vital relations to other plants and to one another that it is difficult to classify them. Indeed, there is no logically recognizable correlation of any of the parasitic characters of the species in question with those which pertain to systematic classification. The following synopsis, prepared for the present occasion only, embraces seven groups the characterization of which is, so far as practicable, based upon the manner of parasitism of the members of the respective groups and upon the peculiarities of their life history, especially that phase of it which pertains to germination.

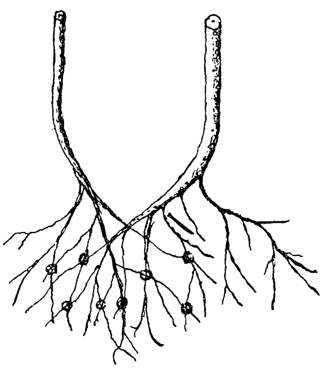

FIG. 1. Diagrammatic pen-sketch, showing the position of haustoria at the places of contact of roots of the parasite and its host. The haustoria are represented by small circles, which are, however, proportionally much larger than natural size.

GROUP I

Seeds germinate upon the ground. Embryo differentiated into cotyledons, radicle and plumule, like normal embryos. Like normal plants also those of this group produce chlorophyl. A part of their roots are attached by sessile haustoria to roots of other plants, from which they obtain ready-made organic substance in liquid form, and a part of them obtain food-sap from the soil in the normal manner. Therefore their parasitism is only partial. Examples: Euphrasia, Pedicularis, Castilleja and many others.

The parasitism of the members of group I, which are

mostly perennial herbs, is confined to limited underground pilfering. It is the simplest form of phenogamous parasitism but it is as persistent and hereditary as are the more complex forms, and it is practised by a large number of genera and species which have numerous near normal relatives. Because they have normal roots and leaves and produce chlorophyl they begin life with the ability to procure an honest living, but they seem to be unable to resist their inherited parasitic inclinations. The development of haustoria at the points of contact of their roots with roots of other plants begins after their germinative birth from a normal embryo and an early stage of full self-support obtained from the soil; but so firmly fixed is the habit of pilfering in these plants that when they have been experimentally forced to live honestly in good soil, but beyond the reach of roots of other plants, they have ceased to thrive, as if they were insufficiently nourished.

### Group II

Parasites attached to the stems and branches of woody hosts upon the bark of which the seeds germinate, being affixed there by their glutinous covering. Embryo differ-

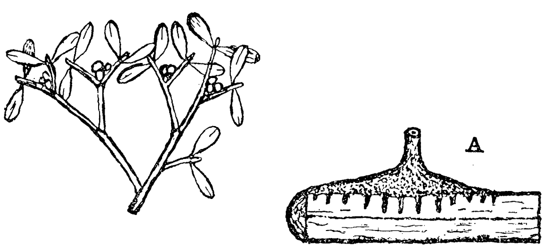


Fig. 2. Pen-sketch of a branch of *Viscum album*, the Old World mistletoe; much reduced in size. *A*. Diagram showing the mode of attachment of the parasite to the host by the sinkers.

entiated into cotyledons, radicle and plumule, and the plant consists of both epitropic and apotropic portions. The latter is differentiated into stem, branches, leaves and fruit, as in normal plants. The leaves, and also the bark of the stem and branches, contain chlorophyl which is produced by the plant itself. The parasite is attached

to the host by "sinkers" which consist of specially modified, but true, rootlets, although in function they simulate the haustoria of other parasites. The sinkers penetrate the bark of the host and obtain nourishment for the parasite from the growing tissues beneath it, much as food-sap is obtained from the soil by normal plants. The parasitism is complete. Examples: The mistletoes.

The members of group II are perhaps the most generally known, at least by name, of all the phenogamous parasites. The family to which they belong, the Loranthaceæ, is a large one, and some of its members differ considerably from the typical forms of mistletoe. Only *Viscum album* of the Old World, and *Phoradendron flavescens*, of the New, however, are chosen to represent group II on this occasion. These mistoes differ from the members of all the other parasitic groups in being perennial woody parasites upon woody hosts, and also in their method of parasitism. That method is peculiar because it simulates grafting, because morphologically its "sinkers" are true rootlets and not haustoria, and because the passage of sap from host to parasite is by those rootlets and not through such harmoniously joined cells as are formed between the graft and its stock. Mistletoes have been known to become parasitic upon other mistletoes, but in their choice of a host they usually give preference to trees that are not botanically related to them. Their structure, both embryonal and mature, is so nearly normal that one might believe them capable of

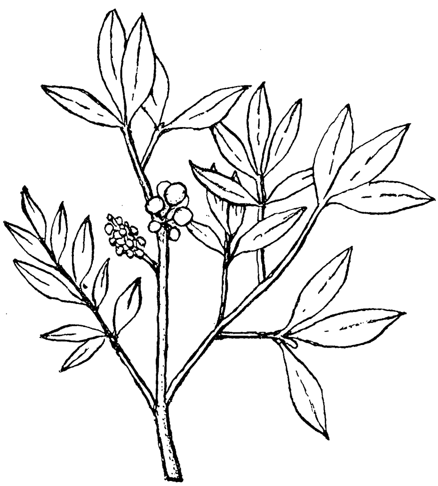

FIG. 3. Pen-sketch of a branch of *Phoradendron flavescens*, the New World mistletoe; two fifths natural size.

leading an honest life in the soil, but so firmly is their predatory habit established by heredity that they never do so. Their seeds will germinate successfully only on the bark of living trees, and their embryos, although structurally perfect, are evidently unable to develop in the soil. When germination of the seed begins the radicle pierces through the dry bark of the host as if driven by some extraneous force; and it sometimes enters the bark of a branch from its under side, showing that gravity is not that impelling force. It lifts the strong bark by its increment beneath, and sends the sinkers into the growing layers. The cells of those layers and the cells of the sinkers become vitally commingled much as do the somatic cells of the scion and stock in common grafting, but not quite so harmoniously. This parasitic root-grafting is remarkable because the parasites and their usual hosts differ from each other in botanical relationship far more than do any scions and stocks that can be artificially grafted with success.

Because the mistletoes obtain full nourishment from their hosts their parasitism is complete, and yet, unlike other completely parasitic phenogams, they produce chlorophyl in their own tissues. The production of chlorophyl by the mistletoes is apparently due to the fact that they have retained morphological representation of true roots, notwithstanding their parasitism. While the mistletoes have retained more of the structure and functions of normal plants than have other completely parasitic phenogams, their draft upon the vitality of their hosts is great, and it doubtless would be more apparent if the latter were less vigorous.

## Group III

Seeds, having the embryo differentiated into cotyledons, radicle and plumule, germinate upon the ground and there produce plants which begin to grow in the soil in the normal manner. By their earlier roots they are partially parasitic after the manner of group I, but, suddenly, the whole plant becomes epitropic and enters the soil bodily by burrowing, much as does the peanut pod

when ripening. It there branches freely, assuming the form of a large complex blanched rootstock, and becomes wholly parasitic. It passes its whole mature life under ground except that some of its branches rise above ground to flower, but those branches always die when the fruit has ripened. Its earlier parasitism is by sessile haustoria, which are soon discarded, and its later parasitism is by haustoria-tipped tendrils, sometimes erroneously

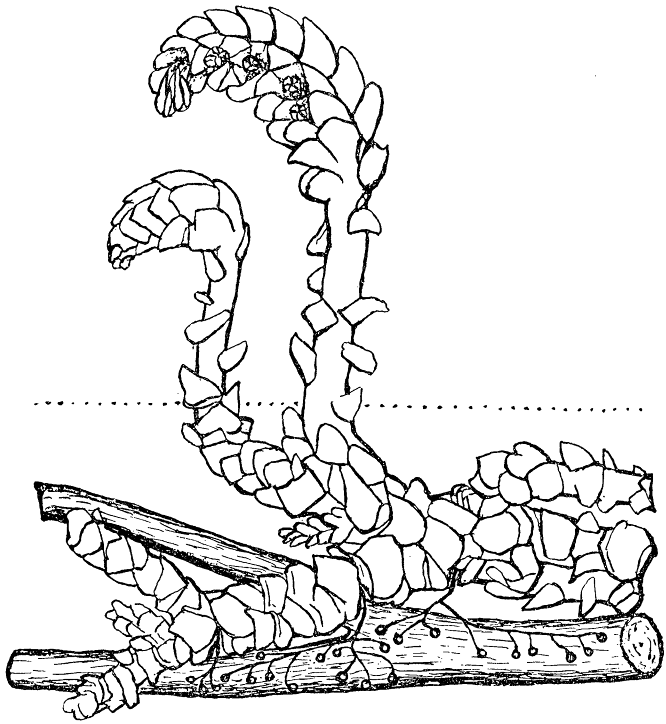

FIG. 4. *Lathræa squamaria*; pen-sketch after Kerner. The dotted line represents the surface of the soil. Only a small part of the underground stems and branches is shown in the figure, together with tendrils bearing the pediculate haustoria.

called roots or rootlets, which issue from the underground stem and branches. No chlorophyl is produced and no functional foliage or functional roots are developed after the plant begins its burrowing. Example: *Lathræa squamaria*. This group has no known American representatives.

The species which has been chosen to represent group III is a European form and is quite distinct in certain respects from even its nearest botanical kindred, and it possesses habits that for variety and extent of abnormality are not surpassed, and apparently not equalled, by any other plant. It begins life normally, as do members of group I, which it then closely resembles. The presence of chlorophyl in the plumule of its plantlet and the development of early rootlets seem to indicate an honest destiny for the plant, but its subsequent acts almost suggest its utter abandonment to a groveling life.

### Group IV

Seeds germinate upon the ground, producing an annual herbaceous plant. Embryo filiform and coiled within a mass of albumen in the seed; not differentiated into cotyledons, radicle or plumule. The resulting plantlet retains the filiform structure of the embryo without differentiation, except that the part which becomes the lower end of the plantlet is slightly enlarged. As the embryo uncoils the larger end enters the ground a little, but sends no rootlets into the soil and therefore derives no true food-sap therefrom. The smaller end points upward and the plantlet elongates as a single thread-like stem until it comes in contact with some freshly growing part of another plant. It there attaches itself by quickly developed haustoria, derives from the helpless host its first sufficient nourishment, and becomes a branching vine. It then reaches out for other hosts by more or less numerous branches, and the part below the first haustorial attachment quickly withers and dies. The branches grow rapidly and bear an abundance of flowers and seed. The plant never naturally produces chlorophyl, and develops neither true roots or functional foliage. The parasitism is complete. Examples: Cuscuta of many American and European species, and Cassytha of many Australian, New Zealand and East Indian species.

The members of groups I, II and III are all developed from perfect embryos, like those of normal plants, their

parasitism and abnormal structures being developed after germination. The remaining four groups are not only deficient in structure at maturity, but they originate from embryos which are also deficient in structure. The first of those four groups to be considered is especially represented in our country by the genus Cuscuta which contains many species, commonly known as dodder. They are often found growing plentifully in fields, thickets and waste places during the summer months, their yellowish tangled masses making them conspicuous among the green vegetation. The embryo of Cuscuta gets very little sustenance from the albumen which envelops it in the seed because the seeds are small; and it is because the plants develop no roots that they get no real nourishment from the soil. Nevertheless, the plantlet grows rapidly, somtimes to several inches in length, before it reaches a host; and although it is so slender it possesses great vegetative vigor. This vigor is conspicuously observable in the subsequent growth of those species which often profusely festoon shrubbery, and even trees, securing their hold upon, and their sustenance from, the tender twigs by means of their haustoria. Other species no less vigorously attack the smaller plants and field crops with which they come in contact.

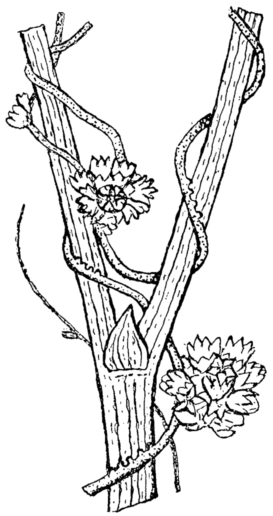

FIG. 5. *Cuscuta Europæa*; parasitic on a hop vine. Sessile haustoria are shown at places of contact of parasite and host.

The parasitism of Cuscuta differs from that of the other groups in being effected by climbing as a vine from plant to plant, and by lateral haustorial contact of the stem and branches of the parasite with those of the host. In the case of the other groups whose parasitism is aboveground the success of the depredating plant depends upon the propitious position which the seeds may accidentally

obtain; but the plantlet of Cuscuta, after its germination upon the ground seems, by the movements of its free end, to start out in search of opportunities. It adjusts its mode of life to prevailing conditions by delaying its own germination about a month later than that of its prospective victims of annual growth, and it is not discouraged by failure of its first effort to find a host. In that case it falls down upon the ground, shriveled and apparently dying, but if soon, or even within a few weeks, some belated normal plantlet should spring up near it, or some growing branch should droop and touch it, the victim is quickly seized upon by the apparently dying plantlet. Such tenacity of life and apparently dominant purpose in a slender, organless mass of vegetable cells is no less than marvelous.

Because the plantlet of Cuscuta develops no root or rootlets it evidently possesses no real representation of the epitropic portion of a normal plantlet, or at best, not more than a moiety of it which lies immediately subjacent to the tropaxis. The rapid upward growth of the filiform plantlet indicates that at least a considerable part of the apotropic portion is therein represented. Moreover, because it has no cotyledons or plumule it follows that the entire plantlet of Cuscuta represents only the stem of the normal plantlet, or that portion of it which comes between the cotyledons and the uppermost rootlets. The accompanying diagram, Fig. 6, illustrates the foregoing statement.

The upper end of *B*, Fig. 6, not reaching above the upper dotted line, indicates that the plantlet of Cuscuta possesses no representative of either cotyledons or plumule. Its downward extension a little below the lower dotted line similarly indicates the fact that its lower end enters the soil a little way, but that it does not represent enough of the epitropic portion of the normal plant to give origin to a root, or any rootlets. This comparison shows that the whole plantlet of Cuscuta represents only the stem of the plantlet of Convolvulus.

The descriptions which have been given in the preced-

ing paragraphs of the structure, germination, life habits and method of parasitism of Cuscuta apply in every important detail to Cassytha. Even the general aspect of the latter plants is such that an American or European seeing them for the first time instinctively regards them as dodders. Nevertheless the structure of their florescence and fruitage leaves no room for doubt of their close

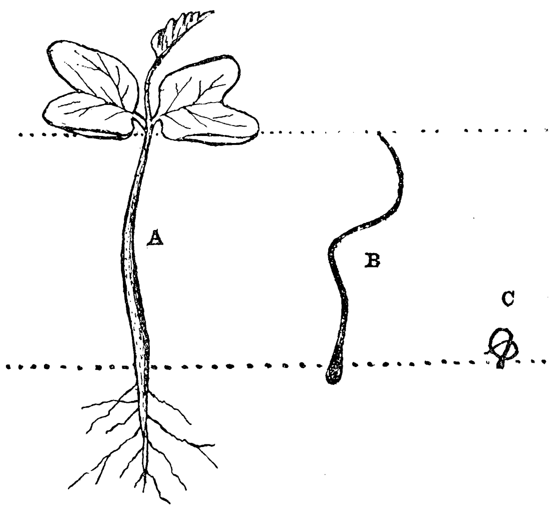


FIG. 6. Diagraphic illustration of the relation of the embryo and plantlet of Cuscuta to the plantlet of Convolvulus.

*A*. An early plantlet of Convolvulus, with its first root and rootlets, its stem, cotyledons and the first leaf of the plumule, not yet expanded.

*B*. The filiform plantlet of Cuscuta of nearly the same stage of growth from the seed as *A*.

The upper dotted line crosses *A* just a little below the place of attachment of the cotyledons. The lower dotted line represents the surface of the soil and also the position of the tropaxis of *A*.

*C*. Embryo of Cuscuta, at the beginning of germination. Much enlarged.

relationship to the Laurel family, while all the species of Cuscuta are nearly related to the Convolvulaceæ.

## GROUP V

Seeds germinate upon the ground. Embryo filiform and not differentiated into either cotyledons, radicle or plumule. Its protruding end, or offshoot, penetrates the soil after the manner of a radicle, sometimes to the depth of several inches, but as it sends off no rootlets it derives no true food-sap from the soil. The upper end, or that

which in the normal embryo would bear the plumule, is not developed. If the descending end comes in contact with no living root of another plant the whole embryo dies, although the soil may be abundantly fertile. If it reaches such a root it becomes attached to it and develops a tuberous mass at the place of contact. From this mass spring outgrowths which penetrate the bark of the root-host and blend intimately with the growing layer beneath it, where they act as haustoria. In this mass, also, by a kind of blastemal germination, buds, or substituent plantlets, are formed which produce the flowering stems. No functional foliage and no true roots are developed, and no chlorophyl is produced.

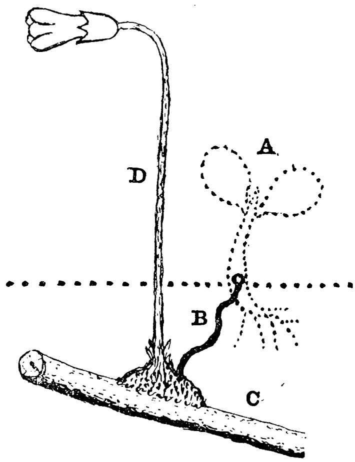


FIG. 7. Diagraphic illustration of the manner of germination and florescence of the broom-rape family, and of the structural relation of its embryo to the normal dicotyledonous embryo.

*A*. Dotted outline of a normal plantlet introduced only for comparison.

*B*. Offshoot of a broom-rape embryo. The upper moiety only may be regarded as representing any part of a normal plantlet, and that represents a portion of the stem. The lower portion of the offshoot is spirally prolonged underground, its free end becoming attached to the root-host by a tuberous enlargement.

*C*. The root-host.

*D*. Flowering stalk of *Aphyllon uniflorum* springing from the tuberous end of the offshoot. The horizontal dotted line indicates the surface of the soil.

The parasitism is complete. Examples: the broom-rapes and related genera.

The parasites of group V belong to the Orobancheæ, the broom-rapes being chosen as typical members. They are vigorous in their growth and aggressive in their parasitism, some of them being very destructive of cultivated crops; especially hemp and tobacco. Like Cuscuta they delay their own germination until their prospective victims have germinated and grown sufficiently to serve their purpose. The seeds of those species which are parasitic

upon cultivated crops seem sometimes to remain in the soil without germination more than one season, and to germinate when a new cultivated crop is planted. The accompanying figure represents the manner of germination of a member of group V and the growth of its flower stem.

Figs. 5 and 7 respectively represent two parasitic plants which, although they originate from physically similar embryos, are so widely different in their mature structure and habits that the following comparison is thought to be desirable. The seeds of both these parasites germinate upon the ground, but the resulting plantlet of one of them grows upward and that of the other downward, in search of a host. The plantlet of Cuscuta grows upward, which is attributed to the assumed fact that its embryo possesses a considerable representation of the apotropic portion of a normal plantlet, and little or no representation of the epitropic portion. No part of the broom-rape embryo grows upward, presumably because it possesses no representation of the apotropic portion of a normal embryo. Its whole embryo seems to represent only a moiety of the stem of a normal plantlet which lies subjacent to its tropaxis and above its rootlets. The bud from which springs the flowering stalk of broom-rape is not a part of the embryo proper, as is the plumule of the normal embryo, but a result of secondary germination.

### Group VI

Seeds germinate only above ground and, like those of the mistletoes, only upon a living woody host; usually upon the stem and branches, but sometimes upon exposed roots. Embryo filiform and without either cotyledons, radicle or plumule. No true roots or functional foliage is developed, and no chlorophyl is produced. The embryo, by its distal or protruding end, when emerging from the seed, sharply and vigorously penetrates the bark of the host and sends haustorial processes into the cambium layer, and even into the alburnum. A single flower, some-

times sessile and sometimes having a short stem, issues from the host at the place of entrance of the embryo. The parasitism is complete.

Examples: The rafflesias and related forms.

One of the most remarkable characteristics of group VI is that the individual plants of many of its species reach the lowest structural limit of the phenogam. That is, each one of such plants consists of a single flower which is sessile upon the bark of the host, or apparently sometimes upon its cambium layer. In other cases the plant consists of a short, single scaly stem besides the flower. The sessile species are examples of flowering plants reduced to the flower alone, assuming that the haustorial processes at its base represent the torus, as they seem to do. While the normal phenogam consists of root, stem and leaves, all of which are necessary to serve the purpose of the coming flower and fruit, the sessile Rafflesias throw the responsibility of all else upon the host and furnish only the reproductive organs for their own perpetuation. They serve that purpose effectively, however, although they are rootless, stemless, branchless and leafless plants. And yet they are no more lacking in vitality than are the most vigorous members of the vegetable kingdom.

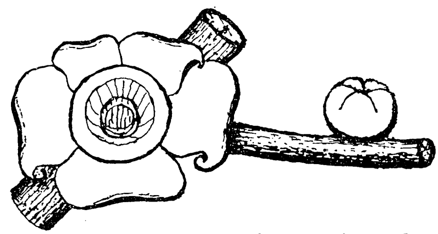

FIG. 8. Pen-sketch of *Rafflesia padma*, together with an undeveloped bud; sessile upon a branch of its tree-host. This species attains a diameter of eighteen inches when fully expanded in flower; but that is only half the diameter of the largest species of *Rafflesia*.

Although the seeds of Rafflesia, like those of the mistletoes, germinate upon the bark of a woody host, their embryo is not of normal structure, as is that of the mistletoes, but is simple and filiform, as is that of groups IV, V, and VII. Because the embryo of Rafflesia is not differentiated, and therefore has not a true radicle; and because it is not able to germinate upon the ground, it is assumed that the protruding end of its offshoot does not represent

the radicle of a normal embryo. If this assumption is correct it follows that the plant is destitute of normal epitropism and that the force with which the offshoot of the embryo pierces the bark and growing wood of the host is an abnormal and violent form of epitropism. It is also assumed that because the embryo of Rafflesia has no plumule the flower does not represent primary apotropism for the plant, but abnormal secondary apotropism as does that of the broom-rapes. The remarkable plants which constitute group VI are divided into many well-defined species and a considerable number of genera. Some of them bear the largest flowers that are known among plants, the largest being more than three feet in diameter, but some are very small. All are natives of warm climates, mostly of Asia, Africa and the adjacent islands. A few American species are known, all of them small. One very small species which is found in Texas and Mexico is sessile in great numbers upon a papilionaceous shrub, and is hardly more than one eighth of an inch in diameter when in full bloom.

## GROUP VII

Group VII consists of a remarkable and varied series of tropical and subtropical phenogamous parasites known as the Balanophoreæ. Some of them have large and showy flowers, and some of them have so great resemblance to fungi that the older botanists regarded them as such. All of them are parasitic upon roots of woody hosts, beneath soil which is usually rich in vegetable mold. The seeds germinate upon the ground. The embryo is not differentiated into cotyledons, radicle and plumule, but it is filiform as is that of groups IV, V and VI, and its offshoot penetrates the ground in a manner similar to that of the broom-rapes. In the manner of their germination and in the underground origin of their flowering stems from a tuberous or amorphous mass, these plants also resemble the broom rapes; but in their florescence and fruitage they are very different. They produce no chlorophyl and they are all without either true roots or functional leaves,

although some of them have moderately large, scaly representatives of leaves.

There are probably other forms of phenogamous parasitism, but the seven fore-mentioned groups are the best

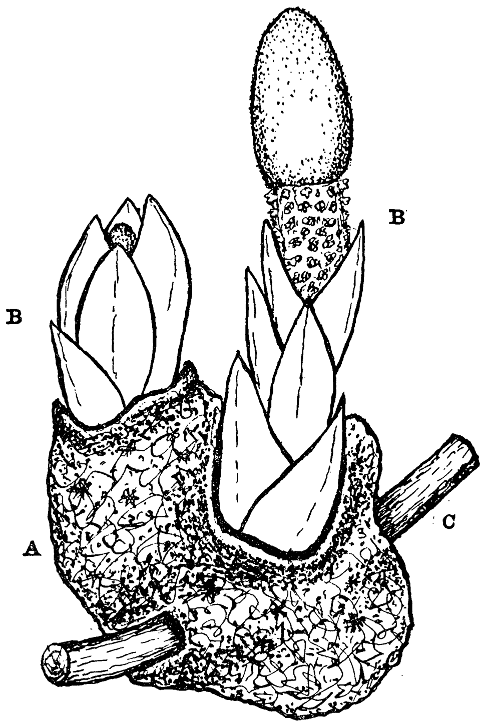


FIG. 9. Pen-sketch of *Balanophora hildenbrandtii*, a native of the Comoro Islands, off the east coast of Africa. After Kerner. One quarter natural size. The leaves of this species, although large, are scaly and not functional.

*A*. Amorphous, fleshy mass. *B*, *B*. Flower stems springing from the mass. *C*. The root-host.

known, and they serve to show that they are all depraved members of the class phenogams, and not predatory members of a separate class.